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NESTED TAXA-AREA CURVES FOR EASTERN UNITED STATES FLORAS

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ABSTRACT. The slopes of log-log species-area curves have been studied extensively and found to be influenced by the range of areas under study. Two such studies of eastern United States floras have yielded species-area curve slopes which differ by more than 100%: 0.251 and 0.113. The first slope may be too steep because the flora of the world was included, and both may be too steep because noncontiguous areas were used. These two hypotheses were tested using a set of nested floras centered in Ohio and continuing up to the flora of the world. The results suggest that this set of eastern United States floras produces a log-log species-area curve with a slope of approximately 0.20 with the flora of the world excluded, and regardless of whether or not the floras are from nested areas. Genera- and family-area curves are less steep than species-area curves and show similar patterns. Taxa ratio curves also increase with area, with the species/family ratio showing the steepest slope.

Key Words: species-area curves, flora, taxonomic ranks

The slopes of log-log species-area curves have been studied extensively because of their theoretical importance in biogeography and practical importance in biological conservation. The slope basically portrays the rate at which the number of species increases with an increase in geographic area. Slopes vary from about 0.1 to 1.0 and are influenced by the range of areas under study. A two-fold difference in slopes is biologically significant because it may indicate real differences in biota or problems in underlying methods. Log-log species-area curves for floras of the eastern United States have been studied by Monk (1971) and Wade and Thompson (1991). Both studies used floras from non-contiguous areas, and found slopes of 0.251 and 0.113, respectively. Monk pointed out that there was an absence of floras of areas between 0.25 and 100 km^2, and Wade and Thompson added some floras in this area range, calling them regional floras. The use of non-nested floras, however, may inflate the steepness of the species-area slope because the floras will be from areas that contain species not in the contiguous areas (Rosenzweig 1995).

Wade and Thompson pointed out that their slope was much less than Monk's for two reasons: in addition to using small floras, Monk used floras of larger areas and from different regions, and also did not have floras in the 0.25 to 100 km^2 range. It appears, therefore, that although Wade and Thompson filled in the gaps in the middle area range, they failed to use nested floras, thereby leading to an inflated slope estimate for the species-area curve for this region. In this study, I have used a recent flora from south-central Ohio (Bennett and Course 1996) to determine whether data from nested floras produce species-area curves with lower slopes than data from non-nested floras.

Species-area curves spanning at least a dozen orders of magnitude on a log area axis, i.e., up to about 10^9 km^2, follow a reverse S-shaped pattern (Williams 1964; Rosenzweig 1995). The slope is steep initially due to sampling effects, then becomes more gradual, and then increases again due to increasing diversity caused by continental-scale biota differences brought about by evolutionary changes in time. The interprovincial variation at larger geographic scales produces species-area curves with the steepest slopes because the biotic provinces rarely exchange species and are thus evolutionarily independent (Rosenzweig 1995). Thus, the use of larger sample areas in the data set may influence the regression slope by making it steeper than it is in the region under study. Monk added the flora of the world to his data set while Wade and Thompson did not, which may partially explain the steeper slope in Monk's study. Here I have studied this effect by comparing regressions with and without the flora of the world.

Taxa of higher ranks than species, e.g., genera and families, represent aggregations of species, so a tabulation of increasing numbers of genera and families is also a tabulation of more species. Even though there are smaller numbers of genera and families than species of plants, it is possible that the numbers of genera and families should increase with area as well, although no data could be found on this in the literature. In addition, the ratios of taxa, which represent taxonomic diversity, have not been examined in relationship to area. The ratios of species to genus, genera to family, and species to family also should increase with area, with the ratio that spans the greatest hierarchical range (species to family) showing the steepest slope. The relationships between taxonomic ratios and area were explored in this study using the floristic data mentioned above, as well as a larger set of 26 other floras.

MATERIALS AND METHODS

The initial data set was composed of eight floras that were completely nested within one another and spanned nine orders of magnitude in area (Table 1). This set centered on a Midwestern national park in south-central Ohio, Hopewell Culture National Historical Park (Figure 1). Floras of 26 other areas were analyzed to expand the sample set. Counts of taxa included species, genera, and families of vascular plants, including the pteridophytes, gymnosperms, and angiosperms. Infraspecific taxa were not included. For some floras, only data on angiosperms were available, and estimates of the numbers of gymnosperms and pteridophytes were made using other references. The totals for the world were calculated by combining the angiosperm numbers of Thorne (1992) with the gymnosperm and pteridophyte numbers of Mabberley (1987). Areas for the floras were obtained directly from the flora publications, atlases, and/or estimated by planimetry from maps. Some counts of taxa were available from the publications directly, while others had to be computed by hand. Ratios of taxa were computed by dividing total numbers of each taxon by the other appropriate taxon. Count and area data then were analyzed by log-log regression using Microsoft Excel. Analyses of covariance using a nested model were performed with Minitab in order to test for significant differences between regression slopes.

RESULTS

The log-log taxa-area curves for species, genera, and families of eight nested floras centered in south-central Ohio and the 26 other floras are shown in Figure 2. The set of all 24 regression slopes (6 taxa and ratios × nested or large data set × with or without the flora of the world = 24) is listed in Table 2. In general, the slopes decrease with an increase in taxonomic level, with the largest decrease in slopes occurring in the nested set of floras with the flora of the world included. Removing the flora of the world, however, decreases the slope as much as adding more floras, an unexpected result. There is virtually no difference in slope between the nested set and large set of floras with the flora of

Table 1. Areas, numbers of plant species, genera and families, and taxonomic ratios for 34 locations. The nested set locations (Figure 1) are indicated in bold print.

Location	Area (km²)	Species	Genera	Families	S/G	G/F	S/F	Source
High Banks Unit	0.0324	174	135	57	1.29	2.37	3.05	Bennett & Course 1996
Seip Unit	0.2146	220	166	65	1.33	2.55	3.38	Bennett & Course 1996
Mound City Unit	0.4858	271	200	80	1.36	2.50	3.39	Bennett & Course 1996
Hopeton Unit	0.6275	238	172	67	1.38	2.57	3.55	Bennett & Course 1996
Hopewell Unit	1	348	229	86	1.52	2.66	4.05	Bennett & Course 1996
Hopewell Park	2.36	442	283	94	1.56	3.01	4.70	Bennett & Course 1996
Ft. Hill Memorial, Highland Co., OH	4.86	650	352	103	1.85	3.42	6.31	Braun 1969
Short Mtn., TN	12	477	262	92	1.82	2.85	5.18	McKinney 1986
Obed Wild & Scenic River, TN	40	733	392	122	1.87	3.21	6.01	Schmalzer et al. 1985
Bernheim Forest, KY	41	859	426	115	2.02	3.70	7.47	Gunn 1959
Savage Gulf, TN	44	677	360	111	1.88	3.24	6.10	Wofford et al. 1979
Mammoth Cave Nat. Park, KY	202	668	415	105	1.61	3.95	6.36	Davies 1955
Wirt Co., WV	609	673	360	106	1.87	3.40	6.35	Bartholomew 1948
Land Between the Lakes, KY-TN	688	789	427	116	1.85	3.68	6.80	Ellis et al. 1971
Giles Co., VA	923	1,026	482	124	2.13	3.89	8.27	Cooperrider & Thorne 1964
Calloway Co., KY	995	1,000	462	129	2.16	3.58	7.75	Woods & Fuller 1988
Ross Co., OH	1,792	1,104	495	122	2.23	4.06	9.05	Cusick & Silberhorn 1977
Monongahela Nat. Forest	6,568	1,353	535	129	2.53	4.15	10.49	Clarkson 1966
Delaware	15,688	2,111	721	142	2.93	5.08	14.87	Tatnall 1946

Table 1. Continued.

Location	Area (km^2)	Species	Genera	Families	S/G	G/F	S/F	Source
Chicago region	28,490	2,530	793	143	3.19	5.55	17.69	Swink & Wilhelm 1994
Southeast Ohio	34,548	2,071	701	141	2.95	4.97	14.69	Cusick & Silberhorn 1977
Ohio	115,996	2,587	820	166	3.15	4.94	15.58	Braun 1989, 1967; Cooperrider 1995; Fisher 1988; J. Furlow, Unpubl. data
Pennsylvania	119,262	3,319	982	179	3.38	5.49	18.54	Rhoads & Klein 1993
Iowa	145,791	1,958	673	141	2.91	4.77	13.89	Eilers & Roosa 1994
Illinois	145,933	2,853	898	172	3.18	5.22	16.59	Mohlenbrock 1986
New England	172,678	2,882	790	151	3.65	5.23	19.09	Seymour 1982
Missouri	178,568	2,438	799	144	3.05	5.55	16.93	Steyermark 1963
Great Plains	1,564,995	2,909	850	161	3.42	5.28	18.07	Great Plains Flora Association 1986
Northeast U.S. & Canada	2,362,836	4,285	1,091	191	3.93	5.71	22.43	Gleason & Cronquist 1991
Northeast & north central U.S. & Canada	2,900,000	5,523	1,133	168	4.87	6.74	32.88	Fernald 1950
Canada	9,970,656	4,102	934	154	4.39	6.06	26.64	Scoggan 1978
North America north of Mexico	21,479,211	21,757	3,164	290	6.88	10.91	75.02	Kartesz 1994
Former Soviet Union	22,101,001	22,270	1,945	216	11.45	9.00	103.10	Czerepanov 1995
World	149,702,000	243,893	13,087	488	18.64	26.82	499.78	Mabberley 1987; Thorne 1992

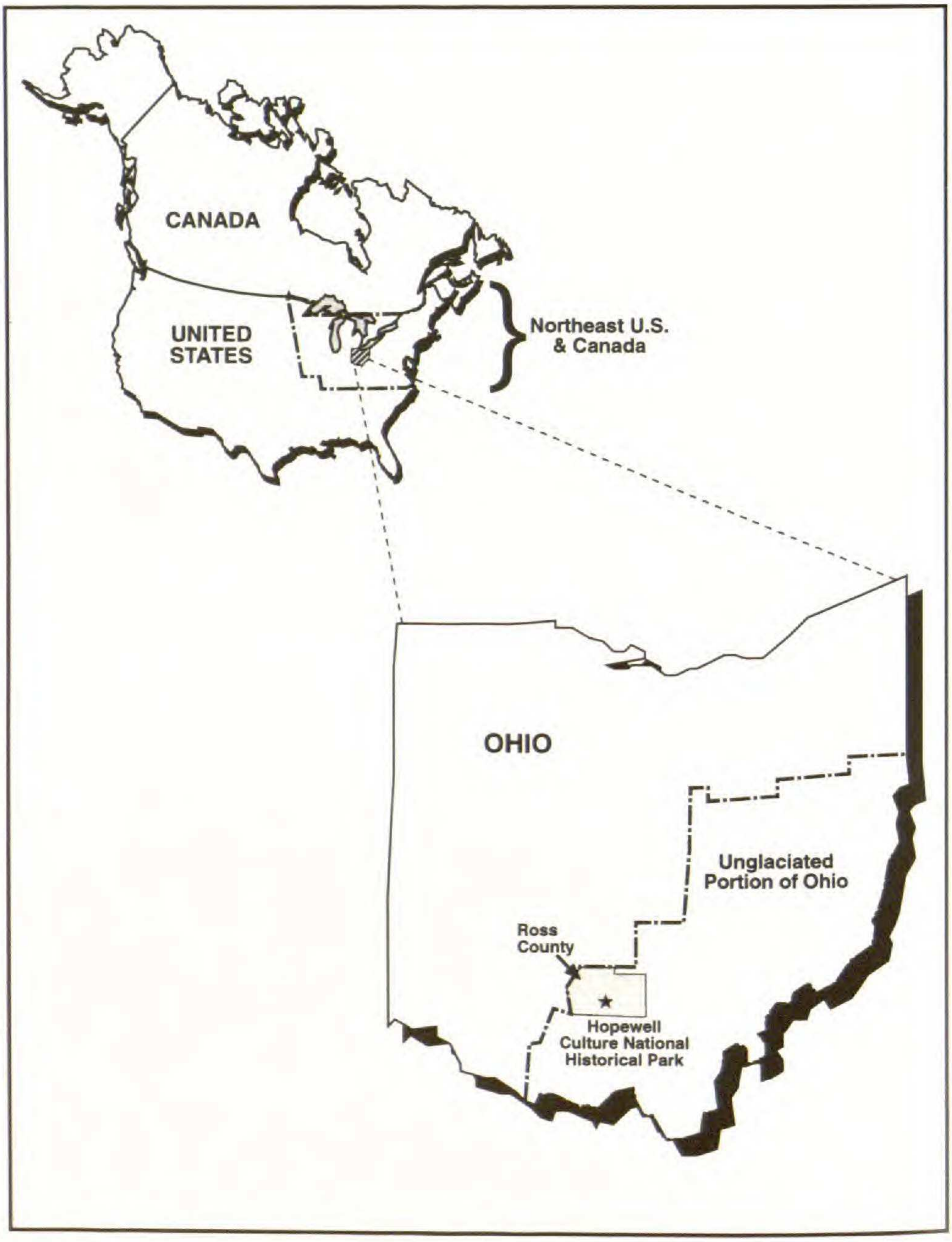

Figure 1. Map of six of the eight nested areas for which floras were used in this study. Missing are the Hopewell Unit of Hopewell Culture National Historical Park because it is too small to show, and the world.

the world removed. The set with the lowest slope for species was for the large set of 34 floras with the flora of the world omitted. The differences between slopes for genera and families followed similar patterns, although to a lesser degree.

The slopes of the taxa-area curves of species, genera, and fam-

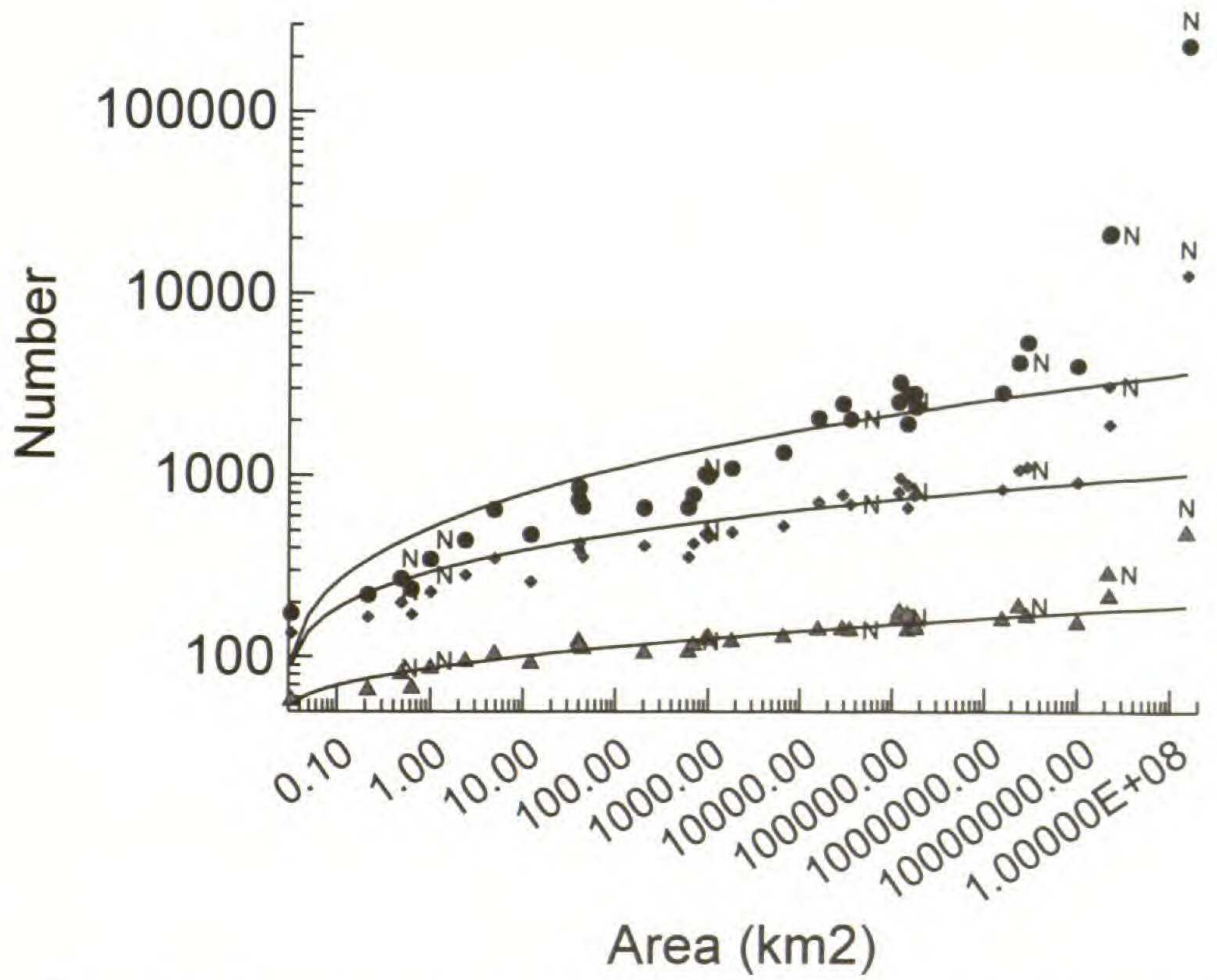

Figure 2. Taxa-area curves for 34 floras of the eastern United States, the former Soviet Union, and the world. Lines through points represent fitted log-log (power) regression equations for species (circles), genera (diamonds), and families (triangles). The subset of eight nested floras in the eastern United States is marked with an N. The three regression equations are: species = 264 area$^{0.22}$ (r^2 = 0.83), genera = 200 area$^{0.13}$ (r^2 = 0.83), and families = 79 area$^{0.06}$ (r^2 = 0.84).

Table 2. Log-log regression slopes of species, genera, families, and their ratios against area for four data sets. Each set of three regression slopes is significantly different ($P < 0.000$).

	Nested Set		Large Set	
Taxon or Ratio	+ World Flora	− World Flora	+ World Flora	− World Flora
Species	0.2800	0.2085	0.2216	0.1942
Genera	0.1724	0.1295	0.1332	0.1159
Families	0.0779	0.0626	0.0629	0.0563
Species/genus	0.1075	0.0790	0.0884	0.0783
Genera/family	0.0945	0.0669	0.0703	0.0597
Species/family	0.2020	0.1459	0.1587	0.1380

ilies within each set (Table 2) were significantly different ($P < 0.000$) in the analyses of covariance, indicating that they are separate regressions. All regression models accounted for 81 to 89% of the variation in taxa numbers (coefficients of determination).

Counts of taxa are measures of floristic richness. Another view of richness is that of taxonomic diversity, which is measured as the ratios of taxa, e.g., species/genus. The taxa-area slopes decline in the order species/family > genera/family = species/genus. Species/family increases with area about twice as much as the other two ratios. Omitting the flora of the world had the same effect on the slope as with the taxa-area curves, and the large set of floras had slopes that were less than those for the nested set.

DISCUSSION

The steepest slope in this study was for the species-area curve in the nested set of floras with the flora of the world included. The slope for the species-area curve for the complete set was somewhat lower, perhaps because many floras were added from smaller areas rather than larger, provincial areas. Regression models for the taxa-area curves explained 82% or more of the variation in numbers of taxa, as found by others (Monk 1971; Wade and Thompson 1991). Regression slopes and coefficients of determination of the taxa ratio curves were slightly lower overall than the taxa-area curves.

The eight-flora data set is highly nested from 1 km^2 to 1.49×10^8 km^2, so none of the increase in slope with increase in area is due to the study areas being noncontiguous. However, it appears that a large part of the increase in slope may be due to including the flora of the world, as Monk did. Without this flora the slopes for the nested set of floras and the larger set of 34 floras are practically the same, and average about 0.20. Adding more noncontiguous floras did not make the slope steeper as expected, probably because many of the floras that were added were for small areas. This data set, then, does not support the hypothesis that including noncontiguous areas will increase the slope of the species-area curve.

The 0.20 value of the slope for floras of the eastern United States is greater than the 0.15 for within-province variation, but less than variation between islands (0.25–0.45) and considerably less than variation between provinces (0.90; Rosenzweig 1995).

This suggests that this collection of floras of the eastern United States is related to area within a slightly larger province than Rosenzweig envisioned, and is not as different as islands would be in the same area range. Therefore, the slope appears more reasonable than the Monk or Wade and Thompson slopes.

The slopes for plant genera and families are all progressively less steep than the species slopes, which is explained by the fact that there are fewer genera and families to begin with, so the curves can't be as steep. Sixty percent of all the families in the world and 24% of all the genera are found in North America.

The taxa ratio curves increase with area much like the taxa-area curves, although only the species/family ratio curve is comparable. This ratio spans two levels of the hierarchy (species, genus, family), while the other two ratios span one level each. This is merely a reflection of the previous observations that the slope for the species-area curve is steeper than the family-area curve, so the ratio of the two must increase as well. Some authors, however, might question the usefulness of this because it is known that taxonomic ratios are manmade entities, and have been subject to arbitrary limits by some taxonomists (Stevens 1997).

To conclude, this set of eastern United States floras produces a log-log species-area curve with a slope of approximately 0.20, regardless of whether the floras are from nested areas or not, and with the flora of the world excluded. Genera- and family-area curves are less steep than species-area curves and follow a similar pattern. Taxa ratio curves also increase with area, with the species/family ratio showing the steepest slope.

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